

COMPETITIVE DISPLACEMENT OF NATIVE MUD SNAILS BY INTRODUCED PERIWINKLES IN THE NEW ENGLAND INTERTIDAL ZONE

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ABSTRACT

During the nineteenth century the mud snail *Ilyanassa obsoleta* was abundant on sand and mud flats, wood works, sea walls, salt marshes, eel grass beds, and cobble beaches in New England. With the exception of sand and mud flats, these habitats are now largely occupied by the introduced periwinkle, *Littorina littorea*. To determine whether *Littorina* competitively displaces *Ilyanassa*, an experimental study was conducted at a site in Barnstable Harbor, Massachusetts where the observed distributions overlapped by 3% by Morisita's index.

Mark-recapture studies suggested that the distribution of *Littorina* was limited by an abiotic factor, currents, through which this species realized its fundamental niche. In contrast, density manipulations demonstrated that *Ilyanassa* emigrated from areas where *Littorina* exceeded densities of 2 to 5 per 0.25 m². *Littorina* limited the upper and lower distribution of *Ilyanassa* and affected its microhabitat distribution in the mid intertidal zone. Habitat displacement was 70% for *Ilyanassa*, calculated as the difference between *Ilyanassa*'s observed distribution and its distribution during littorinid removal experiments. The two species display reciprocal niche overlap with each possessing an exclusive region from which the other is physically restricted. The results suggest that the historical change in the distribution of *Ilyanassa* was due to competitive exclusion by introduced *Littorina*.

INTRODUCTION

Introduced species are numerically dominant members of many marine and estuarine communities in North America, having arrived as fouling organisms on ships and with commercial oysters and by other means since the mid-eighteenth century (Hanna, 1966; Carlton, 1979; Scheltema and Carlton, 1983). Introduced species have been viewed traditionally from an economic perspective with most discussion oriented towards their roles as pests and predators or for mariculture potential (e.g., Elton, 1958; Mann, 1979; Simberloff, 1981). Recently, studies on community structure in marine systems have shown that invading species often competitively displace native species (Farnham, 1980; Carlton, *et al.*, 1982; Race, 1982). Displacement usually involves resource partitioning whereby native species relinquish portions of their habitats or microhabitats to introduced species. In most cases of introduced species in marine systems, however, there are too few descriptions of the earlier community to allow one to assess the degree of competitive displacement.

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In this paper we report the results of experiments which demonstrate competitive displacement of the mud snail *Ilyanassa obsoleta* (= *Nassarius obsoletus*), native to New England, by the introduced periwinkle *Littorina littorea*. These species are the most abundant, large intertidal gastropods of New England. Prior to the arrival of *Littorina*, *Ilyanassa* was described by many naturalists (Say, 1822; Adams, 1839; Gould, 1841; Stimpson, 1865; Perkins, 1869; Verrill and Smith, 1873; Rathbun, 1881). In a comprehensive survey of the Cape Cod region Verrill and Smith (1873) ranked *Ilyanassa* "dominant" on marine and estuarine sand and mud flats, wood works, sea walls, salt marshes, and eel grass beds; "common" on protected rocks, cobble beaches, and pilings of wharves; and "present" in oyster beds. The habitat of *Ilyanassa* has changed markedly since the arrival of *Littorina* although its geographical range along the East Coast (Nova Scotia to northern Florida) has remained unchanged.

History of co-occurrence

Despite the presence of rare subfossil and fossil shells of *Littorina littorea* in Newfoundland and Nova Scotia (Clarke, 1971; Wagner, 1977), the periwinkle was absent from American shores south of Nova Scotia prior to 1860 (Morse, 1880; Ganong, 1886; Kraeuter, 1976; Carlton, 1982) and was probably absent in modern times from all of North America prior to about 1800 (Carlton, in prep.). First recorded in the Bay of Fundy in 1861, *Littorina* reached the north shore of Cape Cod by 1870. It appeared south of Cape Cod at Woods Hole in 1875, in the New York region by 1879, and at Cape May, New Jersey by 1890 (Carlton, 1982; in prep.). To the south, *Littorina* now occurs on isolated rock jetties in Delaware, Maryland, and Virginia, but no populations are established south of about 38° north latitude. *Littorina*, although usually associated with the rocky shore (e.g., Lubchenco, 1978; Carlton *et al.*, 1982), is a predominant organism in marshes and eel grass beds that border soft bottoms, and is also common on such "hard" substrates as wood, algae, rocks, and worm tubes of soft bottom habitats (Rathbun, 1881; Pearse, 1914; Stauffer, 1937; Spooner and Moore, 1940; Dexter, 1945, 1947; Bradley, 1957; Wharfe, 1977; Jüch and Boekschoten, 1980).

The historical progression of *Littorina* west and south along the Atlantic coast is one of the best documented cases of the dispersal of a non-native marine species; this, combined with the superb record-keeping of early naturalists, makes *Ilyanassa* and *Littorina* an exceptional example in which the history of habitat overlap can be reconstructed. North of Cape Cod, *Littorina* was reported to co-occur with *Ilyanassa* on mudflats by Grabau in 1898 (near Boston, MA), on and among eel grass in 1912 by Pearse (1913, 1914; Nahant, MA), and in mud channels by Batchelder in 1915 (New Hampshire). Rathbun (1881), reporting upon observations made at Provincetown, MA in 1879, recorded *Ilyanassa* present on "the inner beaches, and extending up to high tide level," and *Littorina* present "on the shore, on piles of wharves, and . . . on the eel-grass in countless numbers," but did not specifically indicate direct co-occurrence. South of Cape Cod, Balch reported *Littorina* to co-occur with *Ilyanassa* along marsh edges and on mudflats in 1899 (Cold Spring Harbor, NY). Balch (1899), noting the relatively recent arrival of *Littorina* on the New York shore, stated that although it "does not appear as yet seriously to threaten *Nassa obsoleta*, the native competitor for the mudflats," *Ilyanassa* was nonetheless "begin[ning] to yield room." Recognizing differences in diet but without postulating a mechanism, Dimon (1905) predicted that *Littorina* would displace *Ilyanassa* except "on the mud flats, from which it is not likely to be crowded [out] by the newcomer." By 1923 *Ilyanassa* could no longer be found in the Woods Hole region in two of the habitats, cobble and

wood pilings, in which it had been numerically dominant about 1871 (Verrill and Smith, 1873; Allee, 1923). By 1930 Clench was able to report that, all along the shores of bays and inlets of New England, *Littorina* "can be found everywhere between the tide marks crawling over mud and on the blades and among the roots of *Zostera*." Although juveniles are still found around marshes in New England (Brenchley, 1984b), the adult *Ilyanassa*, as Dimon predicted, are generally confined to the soft sand and mud flats (Burbanck, *et al.*, 1956; Dippolito, *et al.*, 1975), the remaining firmer habitats generally being occupied by *Littorina* (Allee, 1923; Dexter, 1945; Burbank, *et al.*, 1956; Dippolito, *et al.*, 1975).

Life habit

The historical account strongly implies the displacement of *Ilyanassa* by *Littorina* but the mechanisms of this displacement have not been previously known. Whether competition for food exists among adult snails, although thought unlikely by Dimon (1905) and by Dippolito *et al.* (1975), is not known. *Littorina littorea* is a facultative omnivorous grazer, consuming both macroalgae and microalgae (Hylleberg and Christensen, 1978; Lubchenco, 1978; Petraitis, 1983), invertebrate eggs (Brenchley, 1982), marsh detritus (Poureaux, 1979), barnacle cyprids in large numbers (Carlton, pers. obs.), and a wide variety of other small encrusting or benthic animals (Blegvad, 1915; Hayes, 1929; Hylleberg and Christensen, 1978; Carlton, pers. obs.). Similarly, *Ilyanassa obsoleta*'s diet encompasses most of these types and other prey as well. *Ilyanassa* has been described as a facultative herbivore/carnivore (Brown, 1969), as an obligate omnivore (Curtis and Hurd, 1979), and as a grazer, deposit-feeder, and detritivore (Connor and Edgar, 1982), ingesting sediment and a wide selection of living and dead animal and plant material (Dimon, 1905; Gurin and Carr, 1971; Atema and Burd, 1975; Haines and Montague, 1979; Abbott and Haderlie, 1980; Curtis and Hurd, 1981; Connor and Edgar, 1982; Race, 1982; Brenchley, pers. obs.).

Dippolito *et al.* (1975) suggested that competition for space is also unlikely, *Littorina* preferring solid substrates and *Ilyanassa* the softer substrata. During the reproductive season, however, *Ilyanassa* move onto solid substrates to lay their egg capsules (Scheltema, 1962; Pechenik, 1978). *Littorina* occupy these substrates and graze attached egg capsules (Brenchley, 1982). Laboratory studies demonstrate that during this process *Littorina* physically interferes with *Ilyanassa*'s egg laying behaviors (Brenchley, 1980, 1984a).

Alternatively, the change in *Ilyanassa*'s distribution may be coincidentally rather than causally related to *Littorina*'s arrival. Chew (1981) has demonstrated that local extinction and displacement of a native pierid butterfly in New England, believed to be due to competitive exclusion by an introduced pierid, is actually the result of shifts in land use and resultant changes in the flora. Alternative hypotheses that would explain the observed shift in *Ilyanassa*'s habitat utilization would therefore include other possible physical or biological changes in the mud snail's environment in the past century. We know of no physical (or chemical) change within *Ilyanassa*'s former or present habitat regime that could cause such shifts nor, in particular, any changes that would affect *Ilyanassa* but no other species. Biologically, at least one other species affecting *Ilyanassa* has also arrived recently in New England: the green crab *Carcinus maenas* (reviewed by Vermeij, 1982a,b) which preys heavily upon *Ilyanassa*'s egg capsules (Brenchley, 1982). Juvenile and adult *Ilyanassa* are prey for a variety of species including birds (Recher, 1966), other snails (Atema and Burd, 1975), crabs (Stenzler and Atema, 1977; Brenchley, unpub. data) and sea stars (Peterson, 1979), but the mud snail is believed to be a generally minor food item. *Ilyanassa* would

not be expected to respond dramatically to manipulations in the density of *Littorina* if predation by other species or other factors were primarily responsible for the change in *Ilyanassa*'s distribution.

The present study was conducted on a sand flat located between a marsh and eel grass bed, one of the few habitats where the two species still coexist. Through mark-recapture experiments, factors controlling the distribution of *Littorina* were studied. Density manipulations of *Littorina* were used to study its effect on distributions of *Ilyanassa*. Elsewhere the behavioral components of the interactions (Brenchley, 1984a) as well as juvenile distributions (Brenchley, 1984b) are detailed; here we focus on patterns and factors controlling adult distributions.

MATERIALS AND METHODS

Patterns of distribution

The study was conducted in Barnstable Harbor, Massachusetts (41°43'N, 70°20'W) between June and September 1980, and between May and November 1981 on a sandy intertidal flat between Indian Trail and Bone Hill Road. A census of adult *Ilyanassa* and *Littorina* was conducted each month along three permanent transects that extended through the intertidal zone from the marsh edge or high intertidal zone, across a sand flat to an eel grass bed at the low intertidal zone, a distance of 150 to 250 m. Individuals on hard surfaces, on the sand, and buried 2 to 3 cm within the sand were counted in 0.25 m² quadrats (n = 4 to 8) every 5 to 10 m along the transects. Additional transects 50 to 100 m in length and paralleling the edges of the marsh and eel grass bed were also censused periodically.

Natural movements of individuals were studied by mark-recapture (Table I). Snails were brought into the laboratory, kept in running sea water, marked, and returned to the field within 3 days of collection. *Ilyanassa* shells were cleaned with a wire brush and the apex was marked with a durable paint (Mark-Tex Corp., NJ). Each shell was numbered with India ink. *Littorina* shells were marked *in situ* or in the laboratory. During June 1981, marked snails were returned to their respective habitats: *Ilyanassa* to the mid-intertidal sand flat, and *Littorina* to the eel grass bed, rocks on

TABLE I

Summary of research protocol, Barnstable Harbor, Massachusetts

Zones	Habitats	Mark-recapture ¹	Manipulations	Fundamental ² niche	Realized niche
Low	Eel grass bed	1502 <i>Littorina</i>	None	August census	July census
Mid	Solid substrata Sand	76 <i>Littorina</i> 781 <i>Ilyanassa</i>	Tide pools: littorine removals, littorine additions, controls	Littorine-removal pools ³	Littorine-control pools ³
High	Marsh sediment Marsh shoots	202 <i>Littorina</i>	Marsh edge: littorine removal plots, control plots	Littorine-removal plots ⁴	Littorine-control plots ⁵

¹ Numbers of marked snails released in June 1981.

² Calculated for *Ilyanassa* only.

³ Mean density on day 7.

⁴ Mean of peak density in each plot.

⁵ Mean of daily means in each plot.

the sand flat, and the marsh edge. Marked individuals were returned to the laboratory for measurement every 6 weeks through November.

Experimental procedures

To determine their effect on the upper limit of *Ilyanassa's* distribution, all *Littorina* were removed daily between 29 June and 7 July, 1980 from three replicate plots, each 2 m long and extending 1.5 m into the marsh (Table I). Two unmanipulated plots, each 1.5 m long and lying between test areas, served as control areas. Numbers of both species were counted daily in 0.25 m² quadrats in all areas; these were approached from the marsh and comparably disturbed by the censuses. On the 4th day of the experiment about 100 *Ilyanassa* were collected from both the marsh and adjacent sand flat at low tide and measured (± 0.1 mm).

Densities of *Littorina* were manipulated in the tide pools to determine their effect on the distribution of *Ilyanassa* in the mid intertidal zone (see Table I). In June 1981 all littorines were collected from one pool (4 to 6 m² area) and added to the center of an adjacent pool that was similar in size and appearance. A third pool was left undisturbed to serve as a control area. Densities of both species were counted prior to these manipulations and also twice during the following week in 8 to 10 replicate quadrats (each 0.25 m²) placed in the center of each pool. This experiment was repeated three times in three weeks in different sets of tide pools. Treatments in 2 pools were reversed after one week by collecting all littorines in an addition-pool and releasing them in a pool from which littorines previously had been removed (Experiments A1, A2).

Censuses of snail distributions in the intertidal zone were used to calculate Morisita's (1959) index of niche overlap. Despite modifications and alternatives to this original index, it remains the least biased when sample sizes are small (Smith and Zaret, 1982) and was appropriate for this study where five habitats were recognized (see Table I). Because the eel grass lay limply at low tide, it was combined with sand into a single habitat. Resource utilization for each species at each monthly census was calculated from the mean density of individuals on each resource summed over the three tidal zones ($n \geq 16$ quadrats per zone, see Table II).

Indices of niche overlap were similarly calculated to determine the extent of habitat displacement (Table I). The "realized niche" (*sensu* Hutchinson, 1957) of *Ilyanassa* and *Littorina* were derived from mean densities in experimental controls and the July census of the eel grass bed when littorines were present. The "fundamental niche" (*sensu* Hutchinson, 1957) of *Ilyanassa* was derived from densities resulting in littorinid removal plots and the August census of the eel grass bed when littorines were absent. Mark-recapture studies indicated that the fundamental niche was the realized niche for *Littorina*; no additional calculations were made for this species.

RESULTS

Littorina distribution

Littorina littorea was most abundant in the upper intertidal zone in the marsh at Barnstable Harbor (Table II) (as is typical of its distribution on soft sediments of Europe and New England). Except during a period between late July and September its distribution extended through the mid intertidal zone, where it was locally abundant on most firm substrates (wood, peat, pebbles, worm tubes, algae), and into the low intertidal eel grass bed where it crawled across sand and blades of grass at low tide.

Mark-recapture studies in the low intertidal zone demonstrated the transient

TABLE II

Mean densities per 0.25 m² of *Littorina littorea* on substrates in three intertidal zones in Barnstable Harbor, Massachusetts, in monthly census in 1981

	May	June	July	Aug.	Sept.	Oct.	Nov.
Upper Zone ¹							
Marsh sediments	48.3	39.7	41.4	89.9	64.8	62.9	31.1
Marsh shoots	21.7	16.3	20.9	30.4	69.2	33.7	8.0
N	32	32	64	64	16	16	32
Mid Zone							
Sand ²	0.9	0.5	0.2	<0.1	0.4	0.1	0.7
Firm objects	3.8	2.3	2.1	0.8	2.3	3.6	3.9
N	32	64	64	64	60	16	16
Low Zone							
Eel grass bed	9.8	9.4	9.4	0.1	0.1	5.3	6.7
N	32	16	16	16	32	16	32

¹ "Sediment" includes bases of stalks; "shoots" refers to snails on blades of cord grass.

² Combined areas with and without *Ilyanassa*; differences not significant ($P > 0.05$) by one-way Analysis of Variance on pooled monthly data.

N, numbers of quadrats counted at low tide.

nature of *Littorina*. *Littorina* were dislodged from "softer" surfaces (e.g., worm tubes, sand, filamentous and "spongy" algae, eel grass) and were often seen rolling along the bottom during incoming tides. These individuals crawled along the sand and often followed mucous trails of conspecifics until a solid object was encountered. Of 1502 marked snails released in the eel grass bed in June 1981, only 40 were recovered there after 1 week and only 3 were recovered after 1 month, all along the marsh edge. Several lines of evidence indicated that widespread transport rather than mass mortality was responsible for this low recovery rate. We also inspected thousands of empty shells in the eel grass and marsh without finding any marked shells; most had been bored by naticid gastropods.

Transport in the mid intertidal zone was documented in August 1980 when approximately 100 unmarked periwinkles were released on each of four occasions in sandy areas where solid substrates were rare and other littorines absent. After 3–4 days on each occasion less than 8 snails were found within a 20 × 20 m area (and these were found on marking-stakes). This dispersion was a result of transport by currents and not active movement, since littorines move only about 60 cm per day on rocky shores (Dexter, 1943) and 20 to 25 m during the autumn on soft substrata (Batchelder, 1915).

In higher intertidal areas where mucous dried during low tide, *Littorina* clung to rocks and marsh grasses. A few individuals marked on rocks and in the marsh in June were still present after 3 months. However, these individuals were also transient as evidenced by rates of colonization. All periwinkles were removed from two rocks and from a log in the mid intertidal zone every 3 to 4 days for a period of 4 weeks in June 1981. Recolonization after 3–4 days ranged from 0 to 14 individuals per ca. 0.10 m², the unmanipulated density, with no change in numbers through time. Daily colonization rates along the marsh edge were obtained from censuses of the littorinid removal experiment, and ranged from 0 to 109 individuals per 0.25 m² per day. In this case colonization rates decreased steadily over the course of the experiment, indicating local rather than widespread transport of individuals.

Ilyanassa distribution

The population of *Ilyanassa obsoleta* in the study area was estimated to contain millions of snails. The population was dominated by adult-sized individuals (Fig. 1A; see Scheltema, 1964) with sparse recruitment in 1979, 1980, and 1981. Beginning in May, as the water warmed, they moved onto solid objects of the mid intertidal zone (Table III) to lay egg capsules, preferring isolated eel grass plants, drift algae, and small islands of marsh peat and avoiding both the eel grass bed and marsh where periwinkles were numerous.

The adult population moved about the 1 km stretch of shoreline of the study site in the mid intertidal zone from March to November. Although Jenner (1956) reports that mud snails in the Harbor aggregate after reproduction ceases, the study population remained in dense aggregations throughout the year, foraging upon their own shells (illustrated by Morse, 1921) and on each other's shell epiflora. Isolated individuals were always rare although individuals moved freely between the aggregations (see also Borowsky, 1979) of which there were usually two or three. General patterns of movement were directed toward the marsh during spring tides from April through July, and toward the eel grass during spring tides occurring in the summer and fall.

In a nursery area near the marsh there was a small group (2–5 thousand individuals) comprised of fast growing, immature snails (<17 mm) which separated from the adults in June and roamed about near the marsh until late August or September when they rejoined the adult aggregations.

During winter months the population of *Ilyanassa* hibernated 5 cm in the sediment in the mid intertidal zone. With littorines present in the low intertidal eel grass bed, the mud snails did not migrate to the subtidal zone as has been reported for populations in other areas (e.g., Batchelder, 1915; Sindermann, 1960; Scheltema, 1964; Stambaugh and McDermott, 1969; Murphy, 1979).

Recapture rates of marked *Ilyanassa* were relatively high: of 781 snails released in June 1981, 419 (53.6%) were recovered in September and 109 (13.9%) in August

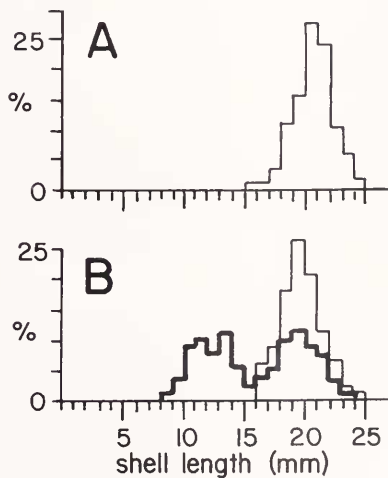


FIGURE 1. Size frequency distributions of *Ilyanassa obsoleta* on the study site in Barnstable Harbor, Massachusetts. A: Sizes of individuals in roving aggregations on the sand flat in July 1981 ($n = 500$). B: Sizes of individuals migrating into the marsh in littorinid removal plots (thin lines) and on the adjacent sand flat (heavy lines) on 3 July 1981 ($n = 100$ each).

TABLE III

Mean densities per 0.25 m² of adult *Ilyanassa obsoleta* in three intertidal zones in Barnstable Harbor, Massachusetts in 1981

	May	June	July	Aug.	Sept.	Oct.	Nov.
Upper Zone ¹							
Marsh sediments	<1	<1	<1	<1	<1	0	0
Mid Zone							
Sand flat ²	89.3	81.6	93.5	61.1	82.6	67.6	81.8
Firm objects ³	1.7	2.6	<1	<1	<1	<1	<1
Low Zone							
Eel grass beds	0	<1	<1	12.0	1.1	0	0

¹ Densities on marsh shoots always zero.

² Densities in areas where aggregations of mud snails were present.

³ Excluding *Ilyanassa* shells.

Numbers of quadrats as in Table I.

1982. Of 200 new snails released in November 1981, 99 (49.5%) were recovered the following August. Observations on recovered snails indicated that the decline in the return rate was largely due to the mark, lost by snail grazing and overgrown by a thick diatom layer; empty shells were always rare during the summers of this study.

Evidence of displacement of *Ilyanassa*

The roving groups of adult *Ilyanassa* rarely entered either the marsh or eel grass bed during the summer migration (see Table III). As evidenced by density relationships, the boundaries between mud snails and littorines were extremely abrupt and rarely did the two species co-occur within a 0.25 m² quadrat (Fig. 2).

Within 24 to 48 h after the removal of *Littorina* from the marsh edge, upwardly migrating *Ilyanassa* moved into test areas of the marsh but they did not enter the control areas (Fig. 3). Maximum densities of *Ilyanassa* were recorded 4 days (plot "E"), 5 days ("A") and 6 days ("C") after the initial removal of littorines. This experiment was performed during *Ilyanassa's* first advance toward the marsh in 1980 and prior to the separation of the immatures and adults. Samples collected on the 4th day showed that all *Ilyanassa* in the marsh were of adult size (Fig. 1B). Adults moved from the edge (lower 0.5 m band) into the marsh (upper 0.5 m band) (Fig. 3). As the neap tide approached, both adult and immature *Ilyanassa* retreated from the general vicinity of the marsh. Observations made underwater at later dates revealed that adult *Ilyanassa* occurred along the bases of marsh shoots but never up on the grass blades as do immature *Ilyanassa* (Dimon, 1905; Brenchley, 1984b).

Use of microhabitats differed where the snails occurred in the mid intertidal zone: *Littorina* were more common on solid objects (Table II) and *Ilyanassa* on sand (Table III). Manipulative experiments demonstrated that *Littorina* had three density-related impacts on the microhabitat distribution of reproductively active *Ilyanassa* within the mid intertidal zone (Table IV). (1) Densities of mud snails did not change following the initial removal of littorines from tide pools, but (2) microhabitat distribution changed within 3 days, and by the seventh day significantly more natives were found on solid objects than in either the pre-manipulated, unmanipulated, or littorinid-addition pools. (3) When numbers of periwinkles were doubled, densities of mud snails had decreased by the third day and were significantly smaller than in control

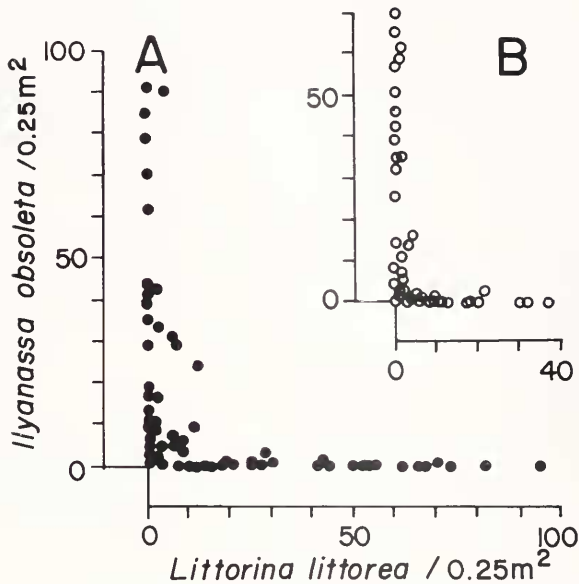


FIGURE 2. Densities of adult *Ilyanassa* as a function of *Littorina* densities in 0.25 m² quadrats in Barnstable Harbor, Massachusetts, June-August 1981: A, upper intertidal marsh edge; B, lower intertidal eel grass bed. Each point represents one quadrat.

pools by day 7. When experimental conditions were reversed in Experiment A2, *Ilyanassa* immigrated into the pool from which they had previously emigrated, and migrated from the new littorinid addition pool (Table IV). This result demonstrates unequivocally that adult *Ilyanassa* avoided *Littorina*. Densities in unmanipulated pools did not change significantly during any experiment.

The overlap in observed distributions of *Ilyanassa* and *Littorina* over the course of the summer ranged from 2 to 5% and averaged 3% (Table V). The experimental studies indicate that, had *Ilyanassa* not avoided *Littorina*, their distributions would have overlapped 71%. The value is not 100% for three reasons: (1) in the absence of *Littorina*, adult *Ilyanassa* did not move onto shoots in the marsh as did *Littorina* (Fig. 3); (2) only a minority of mud snails on the sand flat moved onto solid substrates to reproduce in the absence of *Littorina* (Table IV); and (3) densities of *Littorina* on sand never matched those of *Ilyanassa* (Tables II and III).

DISCUSSION

Results of experimental manipulations of *Littorina littorea* demonstrate density relationships that generally explain observed distributional patterns of *Ilyanassa obsoleta* in the study site. The results show the emigration of *Ilyanassa* from mid intertidal areas when densities of littorines are manipulated (*i.e.*, doubled) to match the conditions found in the marsh and during most of the year in the eel grass beds. Following manipulations to remove littorines from the marsh, *Ilyanassa* expands its distribution upshore; a similar result occurs on cobble beaches in Rhode Island (M. Bertness, pers. comm.) In the one local marsh (Salem, MA) found to contain no *Littorina*, *Ilyanassa* extended throughout to a retaining wall. The results further show that at densities below about 5 individuals per 0.25 m², *Littorina* alters the microhabitat

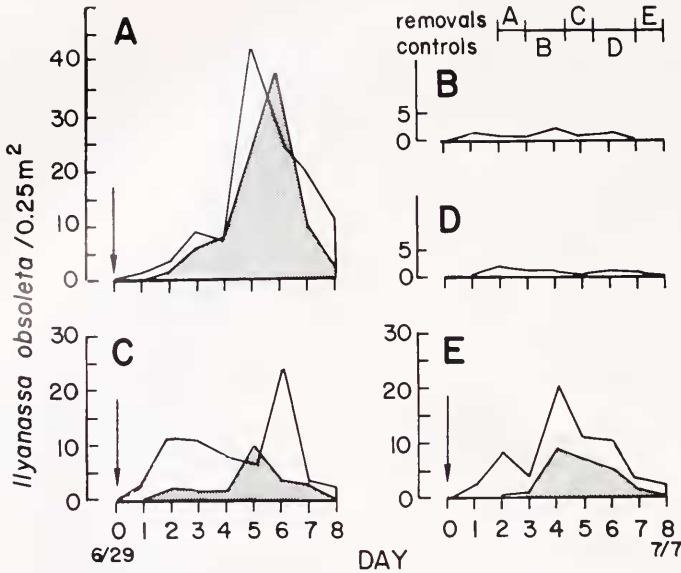


FIGURE 3. Movement of *Ilyanassa* into the marsh in *Littorina*-removal plots (A, C, E) and control plots (B, D) in Barnstable Harbor, Massachusetts in 1980. Position of plots illustrated in upper right corner. Numbers of *Ilyanassa* per 0.25 m² are shown for two 0.5 m wide bands: open figure, lower edge; closed figure, marsh side. Values are means of 4 (removals) or 5 (control) counts per day per area.

distribution of *Ilyanassa*. By excluding the indigenous species from firm substrata, *Littorina* significantly affects the reproductive activity of *Ilyanassa* (Brenchley, 1981, 1984a). In the tide pool experiments, for example, *Ilyanassa* laid significantly more egg capsules in the littorinid removal pools than in littorinid addition pools (Brenchley, 1981, 1984a).

Brenchley (1982) finds that *Littorina littorea* is a major predator on egg capsules of *Ilyanassa obsoleta* in this harbor. Race (1982) documents a similar interaction in San Francisco Bay between a native mud snail (*Cerithidea californica*) and *Ilyanassa obsoleta*, introduced about 1905 (Carlton, 1979). In both cases reproducing individuals are more likely to contribute to the next generation if they avoid habitats occupied by egg predators. If avoidance behaviors of this kind are genetic then only among *Cerithidea* with nonplanktonic larvae are such traits inheritable within local populations. The larvae of *Ilyanassa*, by contrast, have broad dispersal capability (Scheltema, 1962; Gooch *et al.*, 1972). Mechanisms responsible for generating the patterns observed in this study are not likely to have a genetic basis.

Studies of conditioning in *Aplysia californica* by Carew *et al.* (1983) and others have shown that snails can learn to discriminate between tactile stimuli even in a single trial, and can demonstrate the response after several hours. *Littorina* provides tactile stimuli by grazing on shell epiflora of *Ilyanassa*, a behavior which interferes with foraging, locomotory, and reproductive activities of the native species (Brenchley, 1980, 1984a, in prep.). When either *L. littorea* or a native littorinid species (*L. saxatilis*) is on its shell, *Ilyanassa* responds by twisting, a behavior which probably is inherited (see McKillup, 1983, for the polytypic species *Nassarius pauperatus*) since lead weights also elicit the response. Although twisting seldom removes the littorine on the shell, it provides *Ilyanassa* with the opportunity to learn the littorinid scent, or to reinforce prior learning given that the mud snail lives 8 or more years (Jenner

TABLE IV

Densities of *Ilyanassa obsoleta* per 0.25 m² (mean \pm one standard deviation) in tide pools at Barnstable Harbor, Massachusetts, having *Littorina littorea* removed, added, or unchanged in June 1981, compared by one-way Analysis of Variance

Experiment:	A1 (Week 1)	A2 (Week 2)	B (Week 2)	C (Week 3)
<i>Littorina</i> removals				
Overall density				
Initial	26.8 \pm 14.9	2.4 \pm 4.1	42.8 \pm 29.0	43.0 \pm 22.3
Final	28.2 \pm 29.8	31.2 \pm 9.2	35.7 \pm 24.6	27.0 \pm 19.0
F _{1,14}	0.014	57.83***	0.245	3.091
On solid substrata				
Initial	1.2	<0.1	0.9	1.0
Final	3.8	3.1	2.9	3.5
F _{1,14}	16.21***	48.22***	11.51**	29.98***
<i>Littorina</i> addition				
Overall density				
Initial	23.7 \pm 13.2	28.2 \pm 29.8	48.5 \pm 32.4	92.4 \pm 27.9
Final	2.4 \pm 4.1	7.1 \pm 8.0	5.9 \pm 3.9	8.8 \pm 7.4
F _{1,14}	16.66***	3.28	11.93**	58.39***
Unmanipulated controls				
Overall density				
Initial	39.5 \pm 19.6	see B	40.2 \pm 20.9	76.6 \pm 31.5
Final	43.4 \pm 20.4		45.6 \pm 27.6	83.0 \pm 36.6
F _{1,14}	2.911		1.433	2.614

Each n = 8. Conditions of experimental pools in A1 were reversed in A2.

** $P \leq 0.005$; *** $P \leq 0.001$.

and Jenner, 1977). Adult *Ilyanassa* responds to chemical cues, to carrion for example, by extending its proboscis (e.g., Carr, 1967; Brown, 1969). This behavior is observed when adult *Ilyanassa* responds to the littorinid species: after attempting to shake off littorines by twisting, adult *Ilyanassa* will attack the littorine's foot with its proboscis and radula (Brenchley, in prep.). Following sensitization to lead weights, a higher proportion of immature mud snails show this behavior—evidence of a learned response; but adults are slower to probe with their proboscis—evidence that the behavior can be reconditioned.

TABLE V

Index of microhabitat overlap (Morisita, 1959) for *Littorina littorea* and *Ilyanassa obsoleta* at Barnstable Harbor, Massachusetts, during the summer of 1981

Niche	Method	Index
Realized	Seasonal ¹	0.031
Realized	Experimental Controls ²	0.021
Fundamental	Experimental Treatments ²	0.711

¹ Mean of six monthly censuses.

² See Table I.

The proximity of the two species in space depends on the frequency with which *Ilyanassa* encounter *Littorina* on their shells. This frequency depends on two main factors: mobility of littorines, which is largely a function of substrata; and the epiflora on the mud snail shells, which varies both with habitat and snail age. In habitats where littorines are mobile, such as exists throughout the main study site, the critical density is between 12 and 20 littorines per square meter; at higher densities encounters are too frequent and mud snails emigrate. The critical density can be higher on cobble beaches, for example, where *Littorina* are generally less mobile. Types of mud snail shell epiflora correlate with habitat. In sand habitats the epiflora is thickest (up to 2 mm) with strands of *Enteromorpha* common in some regions of the harbor. Thus in muddy habitats *Ilyanassa* can be found in the immediate vicinity of *Littorina* on rocks; this situation rarely occurs in sandier habitats because *Littorina* will move from rock edges to shells of passing mud snails to graze on shell epiflora. We have observed the complete removal of *Enteromorpha* by *Littorina* from shells of a large aggregation of mud snails during a 48 h migration across a rocky area. Finally, *Littorina* rarely grazes on the shells of immature *Ilyanassa* in muddy or sandy regions of the harbor (Brenchley, 1984b). In comparison to adults, juveniles of *Ilyanassa* and *Littorina* have similar foraging behaviors, grazing on microflora on sand and marsh plants. Immature *Ilyanassa* show no evidence of avoiding *Littorina* even when resources are limiting. The change from exploitation to interference competition as the snails age, which coincides with a change from inclusive to reciprocal niche overlap (see Cowell and Fuentes, 1975), is a result of behavioral interactions discussed above.

Unlike the effects of pests and predators (Elton, 1958; Simberloff, 1981), competition leading to displacement or niche partitioning in most cases is subtle. Competition between *Ilyanassa* and *Littorina*, for example, becomes evident through density manipulations but not by comparing the two species' habitat preferences, physiological tolerances, or patterns of distribution (Dippolito *et al.*, 1975). We can estimate from previous faunal descriptions the extent of habitat displacement of *Ilyanassa* by *Littorina*, although we cannot as yet determine the extent to which the abundance of *Ilyanassa* has been affected.

Our studies confirm Dimon's (1905) prediction that the "struggle between [*Littorina* and *Ilyanassa*] may result in a modification of the range" of *Ilyanassa*. Since Dimon's observations in 1905, noting that *Ilyanassa* "act as scavengers for the coast," numerous workers have attempted to elucidate, by observation and experimentation, the precise nature of *Ilyanassa*'s role in the economy of soft sediment shores (Grant, 1965; Mills, 1967; Sibert, 1968; Nichols and Robertson, 1979; Pace *et al.*, 1979; Hunt, 1981; Connor and Edgar, 1982; Connor *et al.*, 1982; Levinton and Stewart, 1982). These studies have demonstrated that *Ilyanassa* exerts significant effects upon community structure, indirectly modifying resources (trophic, spatial, temporal, or otherwise) required by other species, and directly by consuming or displacing potential members of the community. Curtis and Hurd (1981) have speculated in particular upon the full suite of potential impacts by *Ilyanassa* on community structure. We extend Curtis and Hurd's rationale here. We suggest that *Littorina*'s displacement of *Ilyanassa*, while significant to the mud snail, is secondary to the effects that this displacement has had on the benthic community, released from mud snail perturbations. We suggest that there have been major indirect effects in habitats where *Ilyanassa* has been displaced by *Littorina*, whose sediment disturbance (=bioturbation) abilities are minor compared to those of mud snails (Brenchley, pers. obs.); we predict that in habitats from which *Ilyanassa* has been displaced the faunal and floral communities will be similar to experimental manipulative studies that have removed *Ilyanassa* artificially. The introduction of an exotic species has altered community structure not simply

by the modification of distributional patterns of a native species but more profoundly by secondarily modifying the community interactions of the native species as well. As one example, our predictions suggest that polychaete population explosions in mud flats, whose rarity was linked by Levinton and Stewart (1982) to persistent snail populations, would be more common in areas where *Ilyanassa's* local distribution has been contracted by competition. Furthermore, suspecting that the contraction in *Ilyanassa's* distribution due to *Littorina* is associated with the aggregatory behavior of *Ilyanassa* in our study site (Brenchley, 1980), we predict that the establishment and subsequent destruction of dense beds of tubicolous amphipods by aggregations of mud snails (Mills, 1967) will coincide with the abundance of *Littorina* in New England. We conclude that the interpretation of factors controlling the structure of many modern-day marine communities in North America must consider the dynamic interactions of both ecological processes and historical impacts of introduced species.

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